An experimental evaluation of habitat choice in three species of goby (Pisces: Gobiidae)

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The ways in which fish species at similar trophic levels are able to coexist have been examined extensively (see review by Ross 1986 and references therein). However, it is only recently that attempts have been made to use experimental methods to identify the influence that one species may have on the habitat choice of another (e.g., Werner and Hall 1976, 1977; Wiederholm 1987; Magnhagen 1988a, b). While studies of the effects of one species of fish on another in the field have the advantage of providing data on those species in their natural environment, the ability to regulate and manipulate conditions in the laboratory means that laboratory studies can be used to elucidate the role played by individual factors in influencing particular types of behaviour (Crowder 1986). For example, the use of artificial seagrass in laboratory trials provides cover without the confounding effects brought about by the animals and plants usually associated with living seagrass (Bell *et al.* 1985).

Two dominant habitat-types occur in the shallows of Wilson Inlet, a seasonally closed estuary in southwestern Australia, namely unvegetated sand and beds of the aquatic macrophyte *Ruppia megacarpa* (Lukatelich *et al.* 1987), the latter of which may be dense or patchy. The three most abundant demersal species of teleost which occupy these habitats are gobies, each of which shows a greater degree of association with either beds of *Ruppia* or bare sand (Humphries *et al.* 1992; Humphries and Potter 1993). Thus, whereas *Favonigobius lateralis* shows a strong association with bare sand, *Afurcagobius suppositus* and *Pseudogobius olorum* are more often associated with dense and patchy *Ruppia* habitats respectively. Since the above species are all found in the same area in Wilson Inlet, but are associated with different habitat types, a series of laboratory experiments were designed to determine whether the choice of habitat by each of the three goby species is influenced by the presence of either or both of the other species.

The three species were collected from Wilson Inlet and were maintained in 20 l glass aquaria at ambient photoperiod (13.5 h light/10.5 h dark), temperature (20°C) and salinity (ca 30 $^{0}/_{00}$) and fed brine shrimp daily. The experiments were conducted in a square tank comprising 1 m long and 0.5 m high sides. Washed sand was placed in the tank to a depth of 5 cm and covered with water to a depth of 35 cm. Artificial seagrass was placed in one half of the tank and the other half was left bare. To ensure even illumination, two fluorescent lights were positioned above the tank, these were perpendicular to the boundary of the artificial seagrass and bare sand. The artificial seagrass, which was designed to resemble *Ruppia megacarpa*, was constructed from 40 cm lengths of olive-green curling ribbon. Each blade was split into four longitudinal strips and stapled on to a wire mesh at a density of 670 'blades' m^{-2}, a density which simulates the dense *Ruppia* habitat. Prior to experimentation fish were acclimated to the experimental tank for approximately 18 hours, during which time they were not fed. To determine the intervals at which readings should be made, a total of 42 individuals of each species (in groups of 6 individuals) were observed in isolation and the length of time they took to make a 'conspicuous movement' within the experiment tank was noted. A 'conspicuous movement' was one where a fish moved the equivalent of half the length of the tank, i.e., it could have moved from one type of habitat to another. Results showed that, on average, 78% of individuals of each species made a 'conspicuous movement' within 5 minutes.

The number of fish in each habitat was recorded every 5 minutes for one hour in both the morning and afternoon and once every hour for the six hours between these readings. After each hourly reading, the fish's choice of habitat was assessed in response to a disturbance designed to simulate a predator.

All trials were replicated twice, with the combinations randomly assigned to particular days to remove time effects. In the single species experiments, the trials were conducted with densities of 10, 20 and 30 individuals and in those with two or more species, the trials involved 10

individuals of each species. Although the densities recorded in the field were generally at the lower end of the range used for these trials, i.e., 10 individuals m⁻² (Humphries and Potter 1993), it was considered important to use at least this density to provide a sufficiently large expected frequency for statistical purposes (Sokal and Rohlf 1981). Trials with all combinations of species were conducted: i.e., *P. olorum/A. suppositus*, *P. olorum/F. lateralis*, *A. suppositus/F. lateralis*, *P. olorum/A. suppositus/F. lateralis*. Each fish was only used once in the experiments.

The G-statistic was used to test results for significant deviation from expected frequencies. This test being theoretically superior and computationally simpler than the χ^2 test (Sokal and Rohlf 1981). Readings and replicates were tested for homogeneity using an 'interaction' or 'heterogeneity' G-test. If all readings were homogeneous, the results were pooled. In only five of the 78 (6.4%) trials carried out were the replicates not homogeneous. In single species trials, observed frequencies were tested against expected frequencies of 50:50 using a goodness of fit G-test and a pooled G-statistic was calculated. For mixed species trials, observed frequencies were tested against the frequencies obtained using the same number of fish as in single species trials, using a G-test for independence. This type of comparison means that the only difference between the single species experiments and those involving mixed species was the addition of another species.

When on their own *A. suppositus* showed a very strong preference for the seagrass, irrespective of the densities of fish or the time of day. A similar, but less pronounced, choice was generally exhibited by *F. lateralis*. *Pseudogobius olorum* showed no consistent preference for either habitat. In mixed species experiments, *A. suppositus* maintained its strong preference for seagrass, whereas *F. lateralis* reversed its choice of habitat to that of sand in the presence of *A. suppositus*. *Pseudogobius olorum* showed a clear preference for a particular habitat, namely seagrass, only when all three species were together. In all combinations all species sought refuge in the seagrass when disturbed.

In these laboratory experiments, the habitat choice of *A. suppositus* and *P. olorum* when on their own paralleled their distribution in the field, i.e., in both the laboratory and the field *A. suppositus* showed a very strong preference for the artificial seagrass, while in the case of *P. olorum* the lack of any consistent preference for either seagrass or sand in the laboratory is consistent with the greatest densities for this species being recorded from patchy *Ruppia* habitat in the field (Humphries and Potter 1993). In contrast, although *F. lateralis* chose artificial seagrass in the laboratory it was only ever recorded at low densities in *Ruppia* in the field (Humphries and Potter 1993), while in other systems both Shaw (1986) and Bell and Westoby (1986) reported that *F. lateralis* was typically associated with a bare sand habitat.

In the mixed species experiments, the choice of habitat by each of these species was significantly influenced by the presence of other species. The most dramatic effect was seen with *F. lateralis*, which showed a significant increase in the utilisation of sand in the presence of *A. suppositus*. This parallels the distribution of these species in the field and also the situation reported by Wiederholm (1987) for another goby species (*Pomatoschistus microps*), which when alone utilised artificial vegetation, but in mixed species experiments and in the field was found in an open habitat. However, although Wiederholm (1987) reported a shift in habitat utilisation and considered that the small size of *P. microps* may make it vulnerable to displacement by larger, more aggressive species, other workers have found that differences in habitat use are maintained both in the absence and presence of species at the same trophic level and are probably more a function of differences in morphology and species-specific responses to environmental factors (Schlosser and Toth 1984). A comparison of the body lengths in the present study suggests that size alone cannot account for changes in habitat choice. While *A. suppositus* is on average the largest of the three goby species and therefore could conceivably win agonistic interactions with *F. lateralis* if size was the sole criterion, it did not affect the habitat choice of *P. olorum*, the smallest of the three species. Furthermore, the presence of *F. lateralis* appeared to lead to a greater number of *A. suppositus* entering the artificial seagrass. Thus, there would appear to be a mutual interaction between *F. lateralis* and *A. suppositus*. The fact that *A. suppositus* shows a very strong preference for seagrass would probably make it difficult to displace from this habitat. Humphries and Potter (1993) reported that not only did *Afurcagobius suppositus* and *F. lateralis* share several dietary taxa but that they were one of only two pairs amongst three gobiid and three atherinid species whose diets were often correlated. Moreover, the similar morphology of the terminal/superior mouths, along with short guts and ambush-type feeding strategy of *A. suppositus* and *F. lateralis* contrast with the sub-terminal mouth, long gut and active omnivorous foraging mode exhibited by *P. olorum* (Gill and Miller, 1990; Gill, 1993; Gill and Potter 1993). These similarities may make competitive interactions more likely between *A. suppositus* and *F. lateralis* than between these species and *P. olorum*.

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